

## SHORT COMMUNICATION

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**Seed drops and caches by the harvester ant *Messor barbarus*: do they contribute to seed dispersal in Mediterranean grasslands?**

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**Abstract** To determine whether the harvester ant *Messor barbarus* acts as a seed disperser in Mediterranean grasslands, the accuracy level of seed processing was assessed in the field by quantifying seed drops by loaded foragers. In the vicinity of exploited seed patches 3 times as many diaspores were found as in controls due to seed losses by foragers. Over trails, up to 30% of harvested seeds were dropped, singly, by workers but all were recovered by nestmates within 24 h. Seeds were also dropped within temporary caches with very few viable diaspores being left per cache when ants no longer used the trail. Globally, ant-dispersed diaspores accounted for only 0.1% of seeds harvested by *M. barbarus*. We discuss the possible significance for grassland vegetation of harvester-ant-mediated seed dispersal.

Ants are important seed predators in deserts or semi-arid areas (Tevis 1958; Brown et al. 1979; Davidson et al. 1985; Detrain and Pasteels 2000; Detrain et al. 2000) but they are also widely recognised as seed dispersers in a variety of habitats (Davidson and Morton 1981; Buckley 1982; Beattie 1985; Hughes and Westoby 1992; Levey and Byrne 1993). Evolutionary interactions between ants and plants have even led to seed morphological specialisation such as elaiosomes, which are attractive to ants and encourage dispersal of myrmecochorous plants to a “safe site” for germination and growth (Sernander 1906; Bond et al. 1991; Westoby et al. 1991). The effect of ants on plant dispersal is however not restricted to myrmecochores, since non-elaiosome-bearing seed species that are harvested by ants can ultimately be dispersed at long distances from the

parent plant within the galleries or on the refuse pile of their nest (Beattie and Culver 1982; Rissing 1986; Kaspari 1993). Such dispersal of seeds by harvesters may have preceded myrmecochory during the co-evolution of ants and plants (Rissing 1986). Other possible benefits from harvester ants were not considered. Indeed, the “mistakes” they make, i.e. the seeds they lose along the way, may contribute to plant dispersal and may somewhat compensate for the damage caused by predation. Here, we explore whether ant-mediated dispersal of seeds occurs during the return trip of foragers to their nest.

We observed, from April to June 1997, colonies of the Mediterranean harvester ant, *Messor barbarus*, located at Vidauban (southeastern France). Grasses and a variety of annuals dominated the cover of the study site but sclerophyllous trees (umbrella pine) and evergreen shrubs (e.g. lavender, thyme, juniper) were also present. We assessed the dispersal of seeds by *M. barbarus* foragers, which may occur at three stages of their homeward trip. Harvester ants may drop their load before they reach the foraging trail in the vicinity of the exploited seed patch, while they walk on the trail, or when they encounter a temporary seed cache located on the foraging path. As harvester ants can carry whole fruits and remove the seed from the inedible parts inside the nest, the term “seed” refers without distinction to fruits or seeds that are retrieved by the ants.

**Seed drops outside the trail, near the exploited seed patch**

Outside trails, foragers that dropped their seeds were easily overlooked since the vegetation cover often hid them. Therefore, ant-mediated dispersal of seeds in the vicinity of the discovery site was globally assessed by comparing the numbers of seeds present over the soil surface of trail-centred quadrats to those found in adjacent controls. Sampling was as follows: two 1 m × 0.2 m plots were established approximately 2–3 m apart as

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**Table 1.** Seed drops outside trails, found over the soil surface of trail-centred or control quadrats after foraging activity had ceased ( $n$  number of trails observed). The mean ( $\pm$ SD) numbers of seeds found in trail-centred plots were compared to controls by

a Student  $t$ -test for paired samples (significance level 0.05). Only seed species that were observed in at least four different plots are reported in the table

Seed species	Plant family	Total number (%) of seeds in all trail-centred quadrats		Number of seeds per quadrat			
		All seeds	Viable seeds	Control (mean $\pm$ SE)	Trail-centred (mean $\pm$ SE)	$n$	Paired $t$ -values
<i>Gaudinia fragilis</i>	Poaceae	157 (18.5%)	55 (22.3%)	3.3 $\pm$ 1.5	17.4 $\pm$ 4.0	9	$t=4.1$ $P=0.003$
<i>Holcus lanatus</i>	Poaceae	157 (18.5%)	2 (0.8%)	0	40.0 $\pm$ 27.6	4	$t=1.4$ $P=0.24$
<i>Agrostis pallida</i>	Poaceae	146 (17.2%)	32 (12.9%)	4.5 $\pm$ 2.1	17.6 $\pm$ 4.7	8	$t=2.6$ $P=0.037$
<i>Juncus capitatus</i>	Juncaceae	122 (14.3%)	72 (29.1%)	3.0 $\pm$ 1.3	15.2 $\pm$ 11.9	8	$t=1.15$ $P=0.29$
<i>Tuberaria guttata</i>	Cistaceae	90 (10.6%)	19 (7.7%)	3.4 $\pm$ 1.2	9.0 $\pm$ 5.2	12	$t=1.2$ $P=0.27$
<i>Vulpia myuros</i>	Poaceae	29 (3.4%)	9 (3.6%)	0.7 $\pm$ 0.2	4.8 $\pm$ 2.4	6	$t=1.7$ $P=0.14$
<i>Crepis</i>	Asteraceae	28 (3.3%)	7 (2.8%)	2.2 $\pm$ 1.4	3.5 $\pm$ 1.9	8	$t=2.2$ $P=0.06$
<i>Aira</i> sp.	Poaceae	24 (2.8%)	6 (2.4%)	2.5 $\pm$ 1.6	6.0 $\pm$ 3.0	4	$t=0.9$ $P=0.42$
<i>Mibora verna</i>	Poaceae	7 (0.8%)	7 (2.8%)	1 $\pm$ 0.4	2.8 $\pm$ 0.9	5	$t=1.7$ $P=0.17$
<i>Moenchia erecta</i>	Caryophyllaceae	7 (0.8%)	7 (2.8%)	1.2 $\pm$ 0.5	2.3 $\pm$ 0.8	6	$t=1.9$ $P=0.11$
<i>Plantago</i> sp.	Plantaginaceae	4 (0.5%)	4 (1.6%)	1.7 $\pm$ 1.2	2.0 $\pm$ 0.6	4	$t=0.3$ $P=0.76$
<i>Avena fatua</i>	Poaceae	3 (0.3%)	0 (0%)	0.2 $\pm$ 0.2	0.75 $\pm$ 0.25	4	$t=1.0$ $P=0.39$
All seed species		851 (100%)		15.4 $\pm$ 3.8	53.2 $\pm$ 11.1	16	$t=3.8$ $P=0.002$
All viable seed species			247 (100%)	5.9 $\pm$ 1.6	16.1 $\pm$ 4.8	16	$t=3.0$ $P=0.009$

soon as a new foraging trail was detected. The first plot was centred on the end of the foraging trail; the second (control plot) was chosen in an area of similar exposure, substrate and vegetation cover but in which no seed harvesting by ants occurred. The soil surface of both plots was carefully surveyed: all seeds detectable by eye were counted, removed, stored in vials, identified to species and checked for viability under a binocular microscope. Two successive measures were carried out: firstly at the beginning of foraging when the trail was detected, and secondly when the trail was no longer followed by foragers. Between-plot differences in the amount of plant diaspores provided us with an estimate of seed dispersal exclusively due to the activity of harvester ants. The sampling procedures described above were repeated over 16 different trails.

At the beginning of foraging, the numbers of seeds found in control plots were significantly correlated with those in trail-centred plots (paired samples correlation,  $r=0.828$ ,  $P<0.001$ ), but the correlation was weaker and not significant after several days of harvesting activity when the trail was no longer followed (paired samples correlation,  $r=0.463$ , NS). Indeed, both the total number of seeds and the number of viable diaspores were, significantly, 3 times higher in trail-centred plots than in controls (Table 1). The same proportion of viable seeds (around 30%) was however found in both plots, suggesting that foragers do not selectively drop seeds with no consumption value. Five species each accounted for at least 10% of all seeds dispersed outside trails, in the vicinity of exploited seed patches (Table 1). They were more frequently found in trail-centred plots than in controls, though this difference was significant for only two species (French oat *Gaudinia fragilis* and *Agrostis pallida*). When taking into account

only diaspores which had kept their reproductive potential, *G. fragilis* and *Juncus capitatus* species accounted together for half of lost seeds. The abundance among seed drops of species such as *G. fragilis*, *Holcus lanatus*, *J. capitatus* or *Tuberaria guttata* may be related to their intensive exploitation by harvester ants in spring and early summer (Detrain and Pasteels 2000) suggesting seed dispersal by ants could result from chance losses during food transport.

### Seed drops on foraging trails

Preliminary observations showed that, if seeds were dropped on a trail, they were all located at its very end, near the harvested areas. Therefore, we individually followed loaded workers along the last 2 m of trails. We noted whether seeds were dropped and recovered by nestmates within 1 h or within the following 24 h. We also observed whether, after dropping seeds, ants went on their homeward trip or half-turned back towards the exploited seed patch. The rate of seed drops was assessed for eight plant species which either dominated *M. barbarus* seed retrievals (Detrain and Pasteels 2000) or produced cumbersome seeds likely to be lost by ants (*Plantago*, *Vulpia*, *Avena*).

Such seed drops were observed among 17% of the foraging ants and occurred at higher rates (up to one-third of retrievals by ants) for heavy or cumbersome species such as wild oat *Avena fatua* and *Vulpia myuros* (Table 2). All dropped seeds were recovered by nestmates, usually within 1 h (87%). After having dropped their load, most workers (79%) half-turned back instead of going ahead over the trail, and returned to the exploited seed patch.

**Table 2.** Individual seed drops on trails. For each seed species, the number (and percentage) of drops was measured by following 40 loaded foragers. The rates of seed recovery by nestmates and of U-turns are calculated over the total number of observed seed drops

Plant species	Number (%) of seed drops	% Recovered within 1 h	% Recovered within 24 h	% U-turns after drops
<i>Gaudinia fragilis</i>	4 (10%)	75%	100%	75%
<i>Holcus lanatus</i>	2 (5%)	50%	100%	100%
<i>Juncus capitatus</i>	4 (10%)	75%	100%	100%
<i>Tuberaria guttata</i>	7 (17.5%)	100%	100%	100%
<i>Avena fatua</i>	11 (27.5%)	91%	100%	64%
<i>Plantago</i> sp.	6 (15%)	100%	100%	50%
<i>Vulpia myuros</i>	13 (32.5%)	85%	100%	54%
All species	47 (17%)	87%	100%	79%

### Seed drops in temporary caches

We carried out a daily survey of six different nests in order to detect possible seed caches along trails. For each seed cache, we measured its distance from the nest as well as the total trail length. As soon as ants ceased to use the trail, seeds left within the cache were removed, counted, identified to species and checked for viability.

Harvester ants were seen dropping their load on seed piles located on 20% of *M. barbarus* foraging paths ( $n=75$ , Table 3). Trails associated with seed caches were nearly twice as long and more ramified (two branches on average) than trails without seed caches ( $P<0.005$  and  $P<0.02$  for length and number of branches respectively). No significant difference was found in their length of use ( $P=0.34$ ). Only one seed cache was usually found per trail, two being detected on the same foraging path in 3 of 15 cases. Caches were usually located in the last quarter of trail length, on average at 4 m (SD=3.4) from the exploited seed patch. Among the 18 detected caches, 4 were completely emptied by the ants but most of them still contained seeds when foraging activity had ceased over the trail. Ants left a median number of 21 seeds per detected cache (25th and 75th percentiles: 3.5 and 37 seeds) among which only a few were viable (median: 3 viable seeds, 25th and 75th percentiles: 0 and 9.8 viable seeds). Caches were usually polyspecific and contained a median number of five different seed species (25th and 75th percentiles: 3.25 and 5.4 seed species). The majority of viable diaspores left within caches were of *Vulpia*

*myuros* and of grasses such as *Mibora verna*, *Gaudinia fragilis* or *Bromus* sp. Viable seeds of plantain *Plantago* sp., *Juncus capitatus* and *Tuberaria guttata*, which were extensively harvested species (Detrain and Pasteels 2000), were also found within seed caches.

### Discussion

As harvester ants collect seeds from one area and retrieve them to the nest, they may act as dispersal agents and thus, alter the spatial distribution of plant species. *M. barbarus* workers are very efficient at transporting seeds from the discovery site to the main foraging trail. Taking into account flows of loaded ants per minute, daily activity cycles and trail lifetime (Detrain et al. 2000), we roughly estimate that around 50,000 seeds are retrieved on average per foraging trail. We show here that only 0.1% of those harvested seeds are lost and dispersed by ants in the vicinity of exploited seed patch before foragers join the main trail. Seeds that are dropped on trails are all recovered by nestmates and thus do not contribute to plant dispersal. The high rate of U-turns among ants that have dropped seeds on the trail suggests that they participate in an active process of indirect load transfer between nestmates (Ratnieks and Anderson 1999; Reyes and Haeger 1999). Another kind of transport relay occurs on lengthy trails, i.e. the dropping of seeds in temporary caches. The viable diaspores left in such caches roughly account for less than 0.01% of harvested seeds. Those few seeds that are not retrieved for consumption are however left in a microhabitat conducive to increased germination since these shallow surface caches may accumulate water and provide more suitable soil temperatures.

Plant species that have cumbersome morphological seed adaptations, such as the awns of grasses, or that produce heavy diaspores less subject to wind dispersal, are more likely to benefit from the presence of harvester ants since their seeds are more easily dropped and dispersed by foragers. Data are still needed on the fate of seeds dropped by the ants and the ability of these seeds to survive and develop into reproducing adults. Although benefits may be rare and difficult to study we should not assume they are unimportant. In a system in which most seeds die and in which favourable microen-

**Table 3.** Characteristics of trails with or without temporary seed caches. Both types of trails were compared by means of a Student t-test. Significance level: 0.05

	With seed caches mean $\pm$ SD	Without seed caches mean $\pm$ SD	Statistical test $df=73$
No. of trails observed	15	60	
No. of branching points	1.2 $\pm$ 1.2	0.53 $\pm$ 0.8	$t=2.5$ , $P=0.014$
Trail lifetime (days)	5.9 $\pm$ 4.8	4.8 $\pm$ 3.6	$t=0.96$ , NS
Trail length (m)	18.1 $\pm$ 9.2	10.6 $\pm$ 7.5	$t=3.2$ , $P=0.002$

vironments are limiting, rare events such as seed placement in suitable sites may influence seedling recruitment.

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